STUDIES ON THE STELLARIA LONGIPES GOLDIE COMPLEX — VARIATION IN WILD POPULATIONS[1]

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Stellaria longipes Goldie *s.l.* is a very variable species of circumpolar distribution (see map in Chinnappa and Morton, 1974) and wide ecological amplitude. These factors have led previous workers to describe and name many species and varieties within the complex (e.g., Hultén, 1943; Böcher, 1951; Porsild, 1963). However, identification of both living and herbarium material is frequently difficult and uncertain, and the taxa appear not to be clearly differentiated. Other workers (e.g., Polunin, 1959; Anderson, 1959; and Raup, 1947) recognise a single variable species. Cytologically the species is very variable, displaying both euploidy and aneuploidy, with diploid chromosome numbers ranging from 51 to 107; 52, 78 and 104 are the most frequent. There is no correlation between chromosome number and taxonomy (Chinnappa and Morton, 1974; Philipp, 1972). The purpose of the present paper is to explore the range of morphological variation in this species complex, the geographical distribution of this variation and the extent to which the characters are correlated in a manner which might justify the recognition of taxa. We have confined this study to material from North America, a region containing all the main variational trends, and one in which the species complex is most highly developed, widely distributed, and abundant.

MATERIALS AND METHODS

This study is based on material in several of the major North American herbaria (CAN, DAO, TRT, GH) and in the writers' own collections. Over 1500 specimens have been

[1]Based on part of a thesis (Chinnappa, 1973) submitted to the University of Waterloo in partial fulfillment of the requirements for the degree of Ph.D.

examined. The extensive collections in CAN, largely built up by Dr. Porsild for his study of this complex (Porsild, 1963) proved of particular value. The material we have examined came from the whole of the range of the species in North America and contains all the known variational trends and cytotypes. Material from outside North America was also examined, but was not included in the statistics. It shows no significant differences from that found in North America. For reasons of space, the collections studied, and the basic data obtained from them, are not listed in this account.

The characters used in this study include all those regarded as being of taxonomic significance by previous workers. Many of these characters, such as pubescence, and the development of scarious bracts, do not lend themselves to numerical assessment. Pictorial scatter diagrams (a method developed by Anderson, 1949), are a particularly useful means of presenting this type of data, and they provide an effective and concise visual method of demonstrating correlation between characters, or between characters and geographical distribution. Flower size and petal shape are not readily studied in herbarium specimens and were excluded from the present study. Many herbarium specimens do not bear capsules or seeds, due either to their immaturity when collected, or to the adverse climatic conditions under which the plants were growing. This is particularly so in material from the high arctic where the severe climate often damages the developing anthers or curtails the flowering season.

RESULTS

The following are the characters studied in this investigation:

Habit. This ranges from short, compact cushion-like plants found mainly in the arctic, to tall or diffuse plants, or ones with creeping underground stems. The last are often associated with unstable terrain such as gravel slopes and screes. The length of flowering shoots ranges from 2 to

40 cm. with the shorter plants found mainly in the arctic and in the mountain ranges to the south. Two of the extremes are represented by *Stellaria crassipes* Hult. with a compact cushion habit and short flowering shoots, and by *S. arenicola* Raup with long, straggling, diffuse stems, spreading from a central caudex. Mean internode length (see Fig. 1A) was determined by measuring the middle internode on 2 representative mature flowering shoots from each plant. It provides a partial measure of habit, though it does not indicate whether plants are straggling, creeping or erect.

Inflorescence. The number of flowers in the inflorescence varies greatly and ranges from one to many. The mean number was determined for each plant. For purposes of the pictorial scatter diagrams, plants were classified into four inflorescence types:

Type 1. 1-flowered (occasionally 2)
Type 2. 3-flowered (an occasional inflorescence may have more)
Type 3. few-flowered (2-7 flowers) mean 4.5
Type 4. many-flowered (more than 7) mean 10.0

Types 1 and 2 were predominantly associated with *Stellaria monantha* Hultén, *S. laeta* Richards and *S. crassipes* Hultén, types 3 and 4 with *S. longipes* Goldie, *S. stricta* Richards, *S. arenicola* Raup, *S. subvestita* Greene, *S. Edwardsii* R. Br. and *S. Laxmanni* Fisch. These four inflorescence types were fairly evenly represented in the material we examined, their percentage occurrence being 26.1, 27.1, 26.5 and 20.3 respectively.

The presence and absence of scarious bracts in the inflorescence has been considered to be an important taxonomic character by most students of this complex. Plants without scarious bracts have been described as *Stellaria monantha* (when glabrous) and *S. laeta* (when pubescent). Our observations show that 74.25% of the plants we examined had scarious bracts, which were absent in the remainder.

Capsule. Capsule length ranges from 3 to 8 mm. but is usually from 4.5 to 6.5 mm. (Fig. 1B). Capsules always exceed the calyx in length. There is a gradation in capsule colour from straw-coloured through pale brown and brown to black. Straw-coloured capsules are of rare occurrence in most areas, whilst black ones predominate (Fig. 1C).

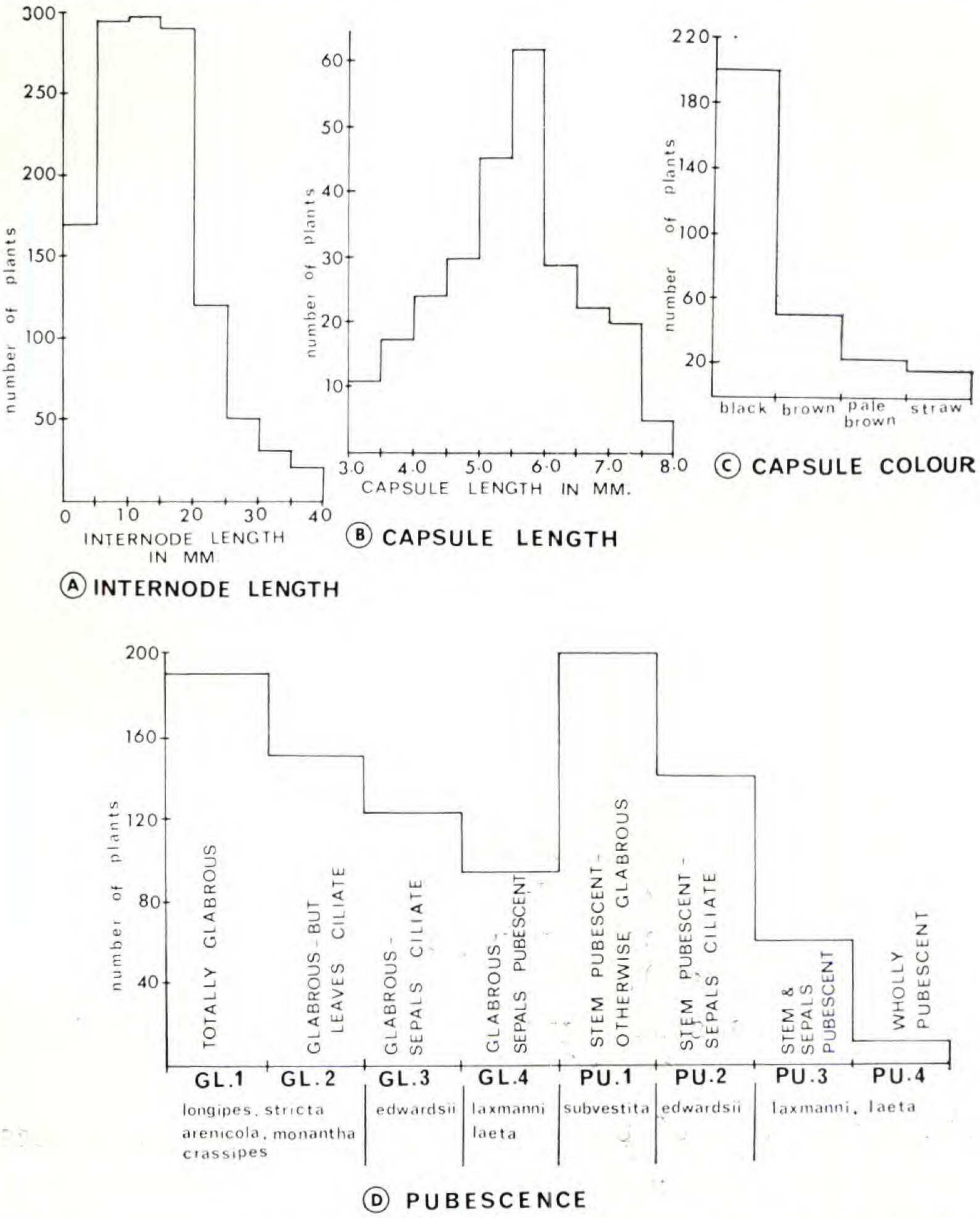

Figure 1. Histograms for measurable characters in the *Stellaria longipes* complex.

The characteristics of the mature capsule teeth (reflexed, spreading or erect) were also recorded. In the plants we studied 77.9% had erect teeth, 18.6% had spreading teeth and 3.5% had reflexed teeth.

Pubescence. This is the most variable character and the complexity in the pattern of pubescence has led to the description of several taxa by previous workers. The aerial parts of the plant vary considerably in respect of pubescence, and in some degree this variation tends to be independent in the different organs. Data were recorded on the following basis.

GL. 1 — totally glabrous (includes *S. longipes, S. stricta, S. arenicola, S. monantha, S. crassipes*).

GL. 2 — glabrous except for the leaves which are ciliate towards the base or on the margins (includes the same taxa as in GL. 1).

GL. 3 — stem and leaves glabrous, sepals ciliate on the margins (includes *S. Edwardsii*).

GL. 4 — stem and leaves glabrous, sepals pubescent on the outer surface (includes *S. Laxmanni* and *S. laeta*).

PU. 1 — stem and leaves pubescent, sepals and pedicels glabrous (includes *S. subvestita*).

PU. 2 — stem and leaves pubescent, sepals ciliate only on the margins, pedicels more or less glabrous (includes *S. Edwardsii*).

PU. 3 — stem and sepals pubescent, leaves and pedicels thinly pubescent (includes *S. Laxmanni* and *S. laeta*).

PU. 4 — plants densely pubescent throughout (includes *S. Laxmanni* and *S. laeta*).

The distribution of plants belonging to these pubescence types is shown in Fig. 1D.

Leaf. Leaves are usually green to dark green in colour, though glaucous ones are of common occurrence in most

populations. The usual leaf shape is lanceolate to linear-lanceolate. However, plants with oblong, ovate, or ovate-lanceolate leaves are not uncommon. Leaf length varies from 3 to 40 mm. and width from 0.5 to 5.0 mm. We decided not to undertake a detailed analysis of leaf measurements when it was observed that leaf proportions changed radically in our cultivated material during the course of development. As a result plants which had ovate leaves in their winter state, produced progressively longer and narrower ones during the flowering season, though the extent of this variation differed from population to population. In our cultivated material this sequence of leaf shape frequently remained intact in mature plants, though in material grown in the wild it is not usually apparent.

Other characters. Several other characters were examined but the data from them proved to be of little value and have been omitted from this account. These characters included the development of a scarious margin on the sepals, seed size and seed sculpturing.

DISCUSSION

Recent authors differ in their treatment of variation in the *Stellaria longipes* complex. Polunin (1959) regarded it as a single very variable species. Böcher (1951) and Hultén (1943) recognised 6 species, Porsild (1963) recognised 9, whilst Hultén (1968) in a subsequent revision, and Boivin (1966) accepted 4 species. All these workers based their taxonomy on the characters used in the present study, laying particular stress on pubescence, leaf shape and the development of the inflorescence and scarious bracts. Our own efforts to use the keys and descriptions of these workers have been only partially successful and many specimens appear to us to be undeterminable. Philipp (1972), in a recent study of material from Greenland, found that about half her specimens were intermediate between 2 or more of the species.

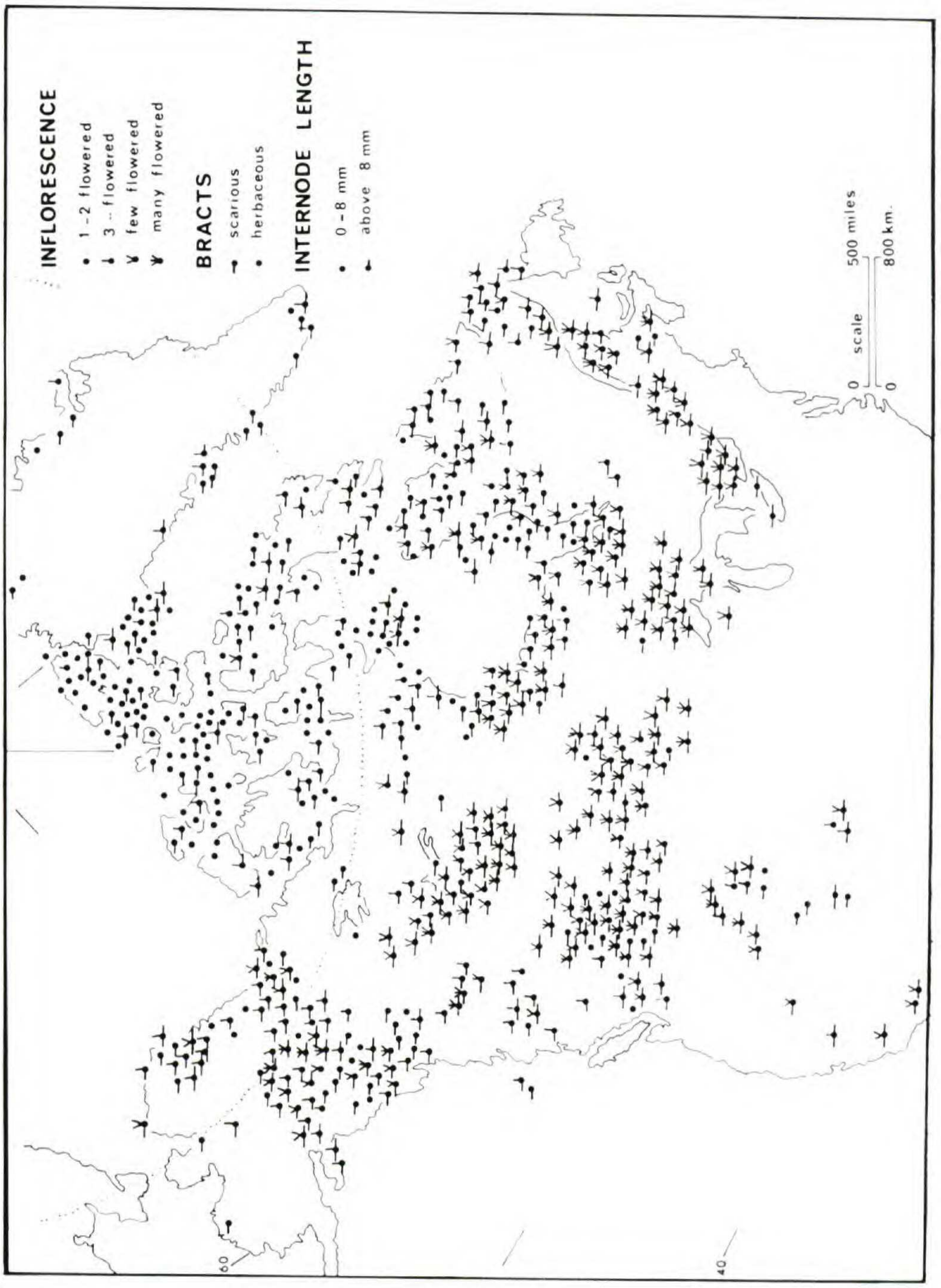

Figure 2. Map showing distribution and association of three characters — inflorescence, bracts and internode length — in *Stellaria longipes*.

For the recognition of taxa at the level of the subspecies and above, not only must there be visible morphological differences, but these differences must be associated, and not distributed at random through the individuals of the population. Furthermore there must be some basis for assuming that these characters are not just phenotypic responses to different environmental conditions. It is appropriate that we examine the pattern of variation in *Stellaria longipes* to determine to what extent the above criteria apply.

All the variation which we have studied in *Stellaria longipes* is of a quantitative nature and shows no discontinuities. This in itself makes the recognition of taxa within this complex of questionable value. The interfertility of the various cytotypes of the *S. longipes* complex has been demonstrated (Chinnappa and Morton, 1974). Hybridization between the cytotypes accounts for the wide range of chromosome numbers found in this complex, and undoubtedly contributes to the lack of discontinuity in morphological characters. Some degree of association of characters is apparent from our analysis of variation. In particular there is a clear tendency for the number of flowers in the inflorescence to be correlated with internode length and the occurrence of scarious bracts (Fig. 2). This correlation, however, has a north to south distribution suggestive either of clinal variation or of a phenotypic response to climate. Thus, low single-flowered plants, lacking scarious bracts, predominate in the arctic, and there is a progressive development in internode length, flower number and scarious bracts in plants towards the south, except in the mountains and other very exposed habitats.

Pubescence also shows a similar north to south trend (Fig. 3) with glabrous plants predominating in the south. However, the pattern of pubescence is complex and usually varies greatly amongst the individual plants of each population. Figure 4 shows this for a population at Churchill, Manitoba. Similar results were obtained from an analysis

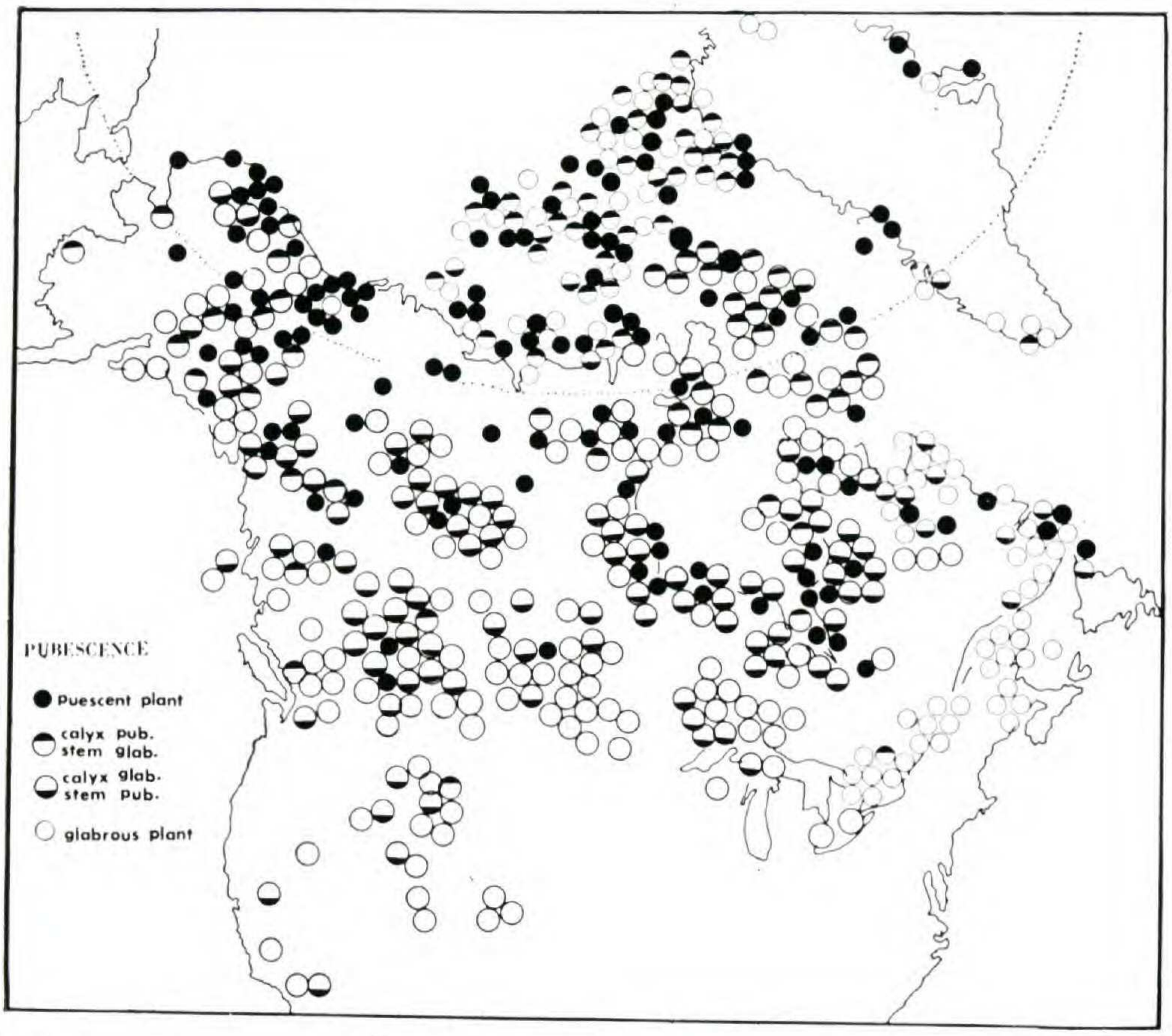

Figure 3. Map showing distribution of pubescence in *Stellaria longipes.*

of other populations. Only occasionally are populations homogeneous in pubescence pattern, and such populations are usually the smaller, more isolated ones. The north to south correlation which exists between pubescence and the characters used in Fig. 2 (bracts, inflorescence and internode) is at best only a broad geographical trend and there is considerable variation within most populations and in most regions. Hence, there is little basis here for the recognition of taxa. This is apparent in Fig. 5 where these characters, together with ones from the capsule, are combined in a single pictorial scatter diagram. It will be noted that the characters used in Fig. 5 include those regarded as being diagnostic for the various taxa included in this species complex.

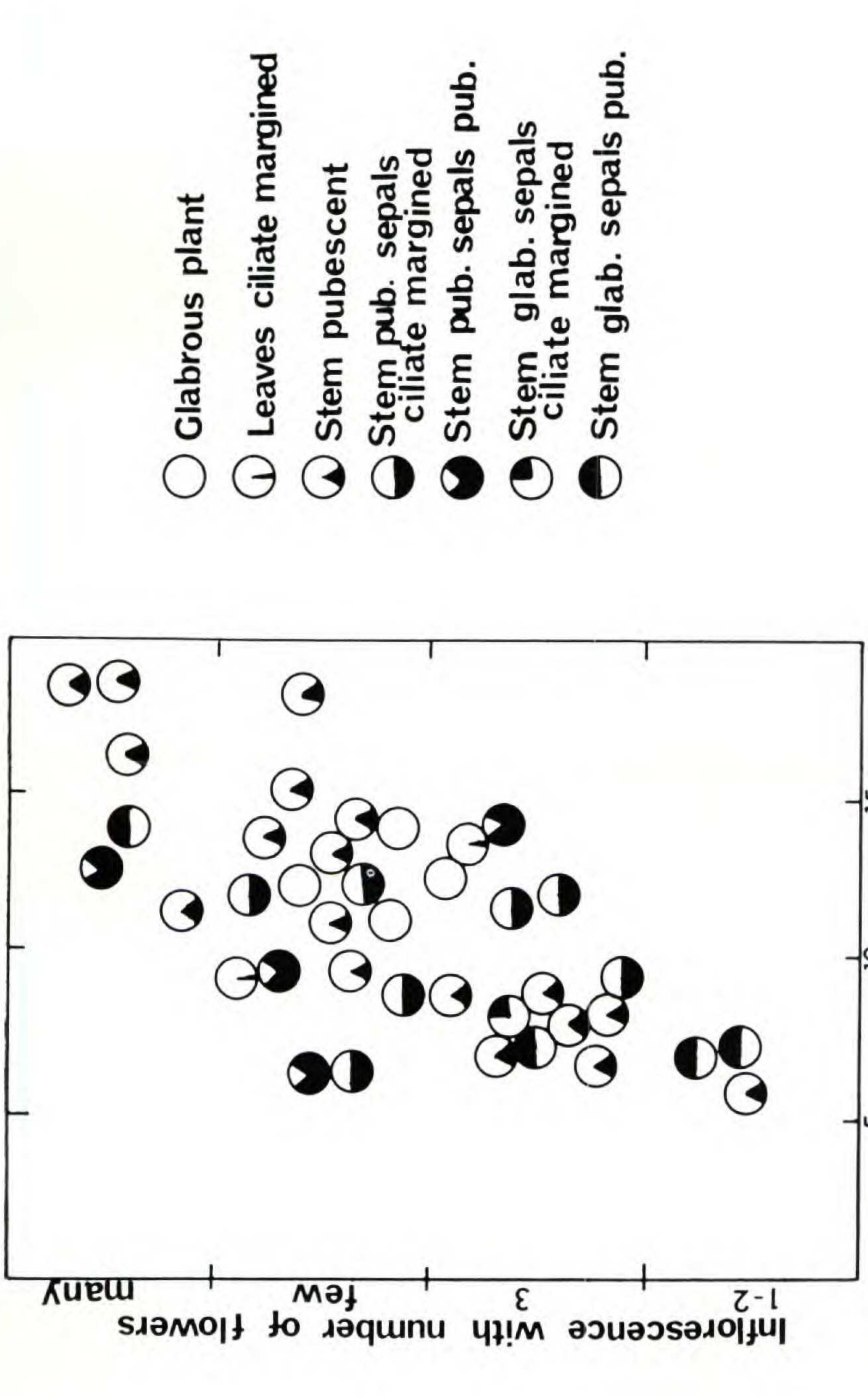

Figure 4. Variation in pubescence amongst a population of *Stellaria longipes* at Churchill, Manitoba. Each circle represents one plant.

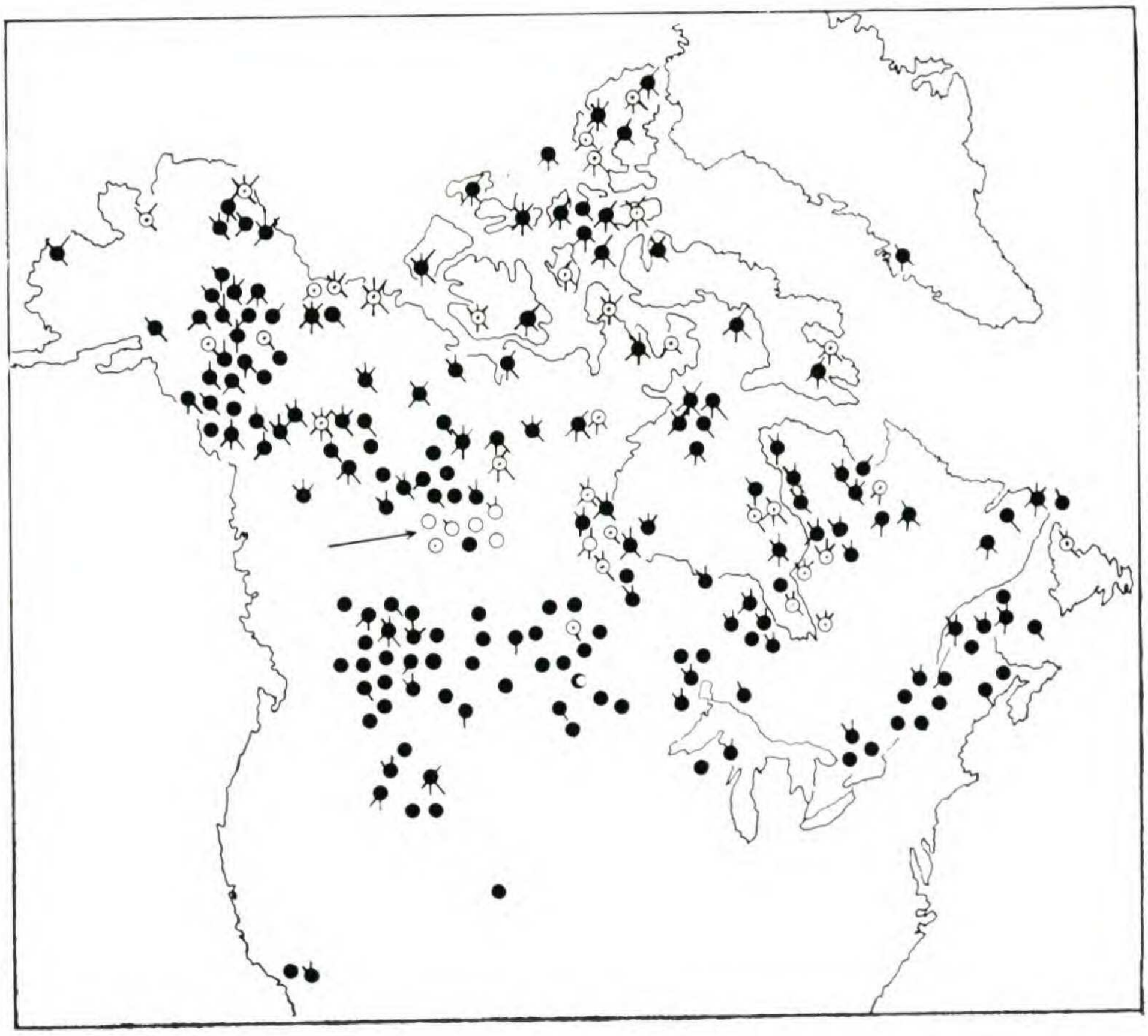

Figure 5. Map showing the distribution and association of capsule, inflorescence, pubescence, habit and internode characters in *Stellaria longipes*. For explanation of symbols see Fig. 6. The arrow indicates the approximate location of Lake Athabasca.

All populations, except those in the region of Lake Athabasca (see Fig. 5), have predominantly black (or dark brown) capsules with erect teeth. In the very specialized habitat of the shifting sand dunes on the south side of Lake Athabasca the situation is reversed, and plants with straw-coloured capsules and reflexed teeth predominate (Figs. 5 and 6). In this population, capsule characters (including a somewhat longer capsule) are associated with a characteristic habit of long, straggling stems with many-flowered inflorescences. Raup (1936) described these plants as *Stellaria arenicola*. However, these characters are not confined to plants from that locality, and

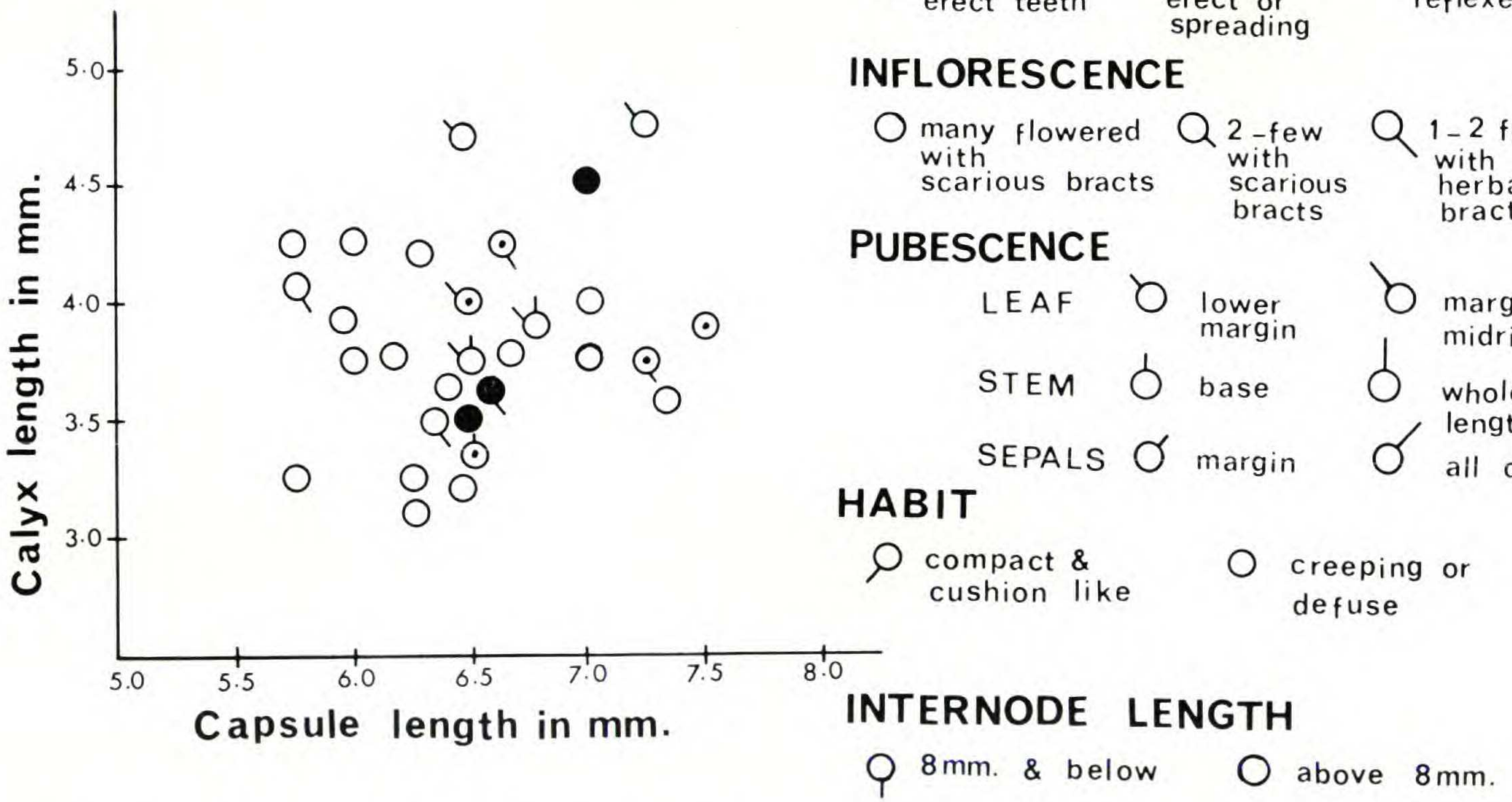

Figure 6. Variation in the Lake Athabasca population of *Stellaria longipes* (*S. arenicola* Raup).

they crop up at random in varying degrees of expression throughout the greater part of the range of the species (Fig. 5). Though paler capsule colour is usually associated with spreading to reflexed teeth, the combination of characters which make up *S. arenicola* (capsule size, colour, teeth, habit and inflorescence) has never been observed outside the Lake Athabasca population. But this population is not discrete and appears to introgress with other forms of *S. longipes* which grow in the vicinity (Fig. 6). Thus the status of *S. arenicola* as a species must be questioned, though some taxonomic recognition may be justified.

Hultén (1943), in describing *Stellaria crassipes*, characterized it as having pale-brown capsules with slightly reflexed teeth, whilst all other taxa were said to have dark brown to black capsules (Hultén did not recognize *S. arenicola*). However, Philipp (1972) observed that out of 42 samples of *S. longipes* s.l. from N.W. Greenland, which included *S. crassipes* Hult., all except one had dark brown capsules. Plants displaying all or some of the other characters, which Hultén associated with *S. crassipes* — short, fleshy, compact, glabrous stems, few-flowered inflorescences, ovate leaves and the near absence of a scarious margin to the bracts — are frequently encountered, particularly in the high arctic, but only rarely are all these characters associated in a single plant, together with pale capsule and slightly reflexed teeth, to produce the characteristic *S. crassipes* as described by Hultén. Hence, we can find little basis for maintaining a taxon, at any level, under the name *S. crassipes*.

It is apparent from this study that *Stellaria longipes* s.l. represents a continuum of variation within and between its many populations. Its characters occur in random combinations, some of which have been favoured with names by previous workers. There appears to us to be little justification for this except perhaps in the case of *S. arenicola* where a distinctive combination of characters persists in association with a very specialized habitat.

CONCLUSIONS

The principal results to emerge from this study are the following:

1. There is considerable variation in the taxonomic characters of *Stellaria longipes* in most of the populations throughout the greater part of the range of the species. This variation is not discrete and is of a quantitative or continuous nature, making the recognition of taxa difficult and of questionable value.

2. There is a clear north to south trend of variation in the following characters — internode length, pubescence, number of flowers in the inflorescence, and the occurrence of scarious bracts. Furthermore, variation in the last 3 characters is usually correlated, but this variation, along with that in leaf shape, is probably under considerable environmental and developmental influence and may not be genetically determined. Thus its taxonomic value is questionable.

3. The populations on the Lake Athabasca sand dunes, named *Stellaria arenicola* Raup, are distinctive and show a sufficiently marked correlation of characters to justify taxonomic recognition. Though these characters occur randomly throughout the range of the species in North America, only at Lake Athabasca are they associated in a high proportion of the individuals in the population. *Stellaria arenicola* appears to introgress freely with other forms of *S. longipes* which grow in the vicinity. Hence, the specific status of *S. arenicola* is questionable and it appears more appropriate to treat it at an infra-specific level within *S. longipes*.

4. A satisfactory understanding of variation in the *Stellaria longipes* complex must await an experimental study to determine its genetic basis and the reproductive biology of the component populations. Such a study has been undertaken and will be reported in a subsequent paper.

ACKNOWLEDGEMENTS

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REFERENCES

ANDERSON, J. P. 1959. Flora of Alaska and adjacent parts of Canada. The Iowa State Univ. Press. 543 pp.

ANDERSON, E. 1949. Introgressive hybridization. Hafner Pub. Co. N.Y. 109 pp.

BÖCHER, T. W. 1951. Studies on the distribution of the units within the collective species of *Stellaria longipes*. Bot. Tidsskr. **48**: 402-420.

BOIVIN, B. 1966. Enumeration des plantes du Canada. Naturaliste Can. **93**: 371-437.

CHINNAPPA, C. C. 1973. A biosystematic study of the *Stellaria longipes* complex (Caryophyllaceae) Ph.D. Thesis. Univ. of Waterloo.

————————, & J. K. MORTON. 1974. The cytology of *Stellaria longipes* Goldie and the evolution of chromosome number. Can. J. Genet. Cytol. **16**: 499-514.

HULTÉN, E. 1943. *Stellaria longipes* Goldie and its allies. Bot. Notiser **1943**: 251-270.

————————. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press. Calif. 1008 pp.

PHILIPP, M. 1972. The *Stellaria longipes* group in N.W. Greenland. Cytological and morphological investigations. Bot. Tidsskr. **67**: 64-75.

POLUNIN, N. 1959. Circumpolar arctic flora. Oxford. 514 pp.

PORSILD, A. E. 1963. *Stellaria longipes* Goldie and its allies in North America. Nat. Mus. Canada Bull. **186**: 1-35.

RAUP, H. M. 1936. Phytogeographic studies in the Athabasca-Great Slave Lake region. I. Catalogue of vascular plants. J. Arn. Arb. **17**: 248-249.

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